# Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites

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Above- and below-ground net primary production was estimated for 40-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands growing on sites with apparently large differences in productivity potential. Aboveground net production was estimated from direct measurements of tree growth; belowground productivity was derived from data obtained by sorting live and dead roots from soil cores used in combination with measurements of root growth on observation windows.

Aboveground net production was 13.7 $t\cdot ha^{-1}$ on the high productivity site and 7.3 $t\cdot ha^{-1}$ on the low productivity site. Belowground dry matter production on the high productivity site was 4.1 $t\cdot ha^{-1}$ compared with 8.1 $t\cdot ha^{-1}$ for the poorer site. On the more productive site, 8% of total stand dry matter production was in fine roots in contrast to over 36% on the poorer site. The difference in total net production (aboveground plus belowground) between the two sites was small (2.4 $t\cdot ha^{-1}$). Apparent differences in aboveground productivity may, to a large extent, result from the need for a greater investment in the fine roots on harsher sites.

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Les auteurs ont mesuré la production primaire nette des parties aériennes et souterraines de peuplements de *Pseudotsuga menziesii* (Mirb.) Franco, âgés de 40 ans, croissant sur deux stations offrant, en apparence, des productivités potentielles contrastantes. La production souterraine nette fut calculée à partir de prélèvements, d'échantillons permettant de séparer les racines vivantes et les racines mortes, et des mesures de la croissance de racines depuis des fenêtres d'observation.

La production aérienne nette de biomasse était de 13,7 $t\cdot ha^{-1}$ sur la station de faible productivité. Les productions correspondantes de matière sèche souterraine dans ces deux stations étaient respectivement de 4,1 $t\cdot ha^{-1}$ et 8,1 $t\cdot ha^{-1}$. Dans la plus productive des deux stations, 8% de la production totale de matière sèche du peuplement provenait des racines fines, comparativement à plus de 36% pour l'autre station. La différence de production totale nette (aérienne et souterraine), entre les deux stations, est faible (2,4 $t\cdot ha^{-1}$). Les différences apparentes de productivité aérienne traduisent sans doute le besoin d'un développement racinaire plus important chez les peuplements croissant dans des stations pauvres.

[Traduit par le journal]

## Introduction

The main objective of this study was to compare primary production by two 40-year-old stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco); one occupying a productive site, the other a relatively poor site. Of particular interest in this research was determining the relative proportion of primary production occurring above and below the soil surface in the two stands. We hypothesized that a greater energy expenditure, in the form of belowground dry matter production, would be required by stands growing on droughty, nutrient-poor sites than by those occupying more productive sites. For this reason, considerable emphasis during this study was placed on examining belowground primary production.

Studies to date indicate a large range in fine root biomass in various forest types. Santantonio et al. (1977) reported fine root (<5 mm) biomass in Douglas-fir forests in Oregon ranging from 8.5 to 10.1 $t\cdot ha^{-1}$. Grier et al. (1981) report fine root biomass (<2 mm) as high as 8.3 $t\cdot ha^{-1}$ in *Abies amabilis* ecosystems in the Washington Cascades. In contrast, Kimmins and Hawkes (1978) found only 1.9 $t\cdot ha^{-1}$ of coniferous fine-root (<6.4 mm) biomass in a mature white spruce and subalpine fir (*Picea glauca* – *Abies lasiocarpa*) stand in interior British Columbia.

At present, relatively little is known about production and turnover of fine roots. Several studies have shown that the standing crop of fine roots in a forest can undergo large seasonal fluctuation (Göttsche 1972; Kohman 1972; Ford and Deans 1977; Harris et al. 1977; Persson 1978, 1979, 1980*a*, 1980*b*; Deans 1979; Grier et al. 1981). In fact, production and turnover of fine roots can amount to over 40% of total dry-matter production by forest ecosystems (Harris et al. 1977; Grier et al. 1981; Ågren et al. 1980). In spite of recent attention, relatively little is known of the range of fine root biomass and production in forest ecosystems; even

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less is known of how site and climatic factors influence the balance between above- and below-ground components of a stand (cf. Santantonio 1979; Persson 1980*c*). Thus, a second objective of this study was to determine how site factors and fine root production are related in a western coniferous forest.

## Site description

This study was conducted at Charles Lathrop Pack Experimental Forest located 90 km southeast of Seattle, Washington, U.S.A., at a mean elevation of 320 m (longitude 122° W, latitude 46° N). The climate at Pack Forest is typical for the Puget Sound lowland. The frost-free growing season ranges from 130 to 180 days; mean January and July temperatures are 2.4 and 18.1°C, respectively. Annual precipitation averages about 1000 mm with over 90% of the precipitation falling between October and June, mostly as rain. Less than 10% of annual precipitation occurs in July, August, and September. Summer relative humidity can be as low as 10%.

Study plots were established on sites supporting low and high productivity stands at Pack Forest. The two sites differed mainly in the soils supporting the two ecosystems; climate, fire, and logging history of the two sites were the same. Both sites were occupied by 40-year-old stands of Douglas-fir naturally regenerated after wild fires. The low productivity stand had developed on an Everett series soil; the more productive stand occupied a Wilkeson series soil.

The Everett series is a gravelly loamy sand derived from pleistocene glacial outwash and is widespread in the Puget Sound region. These outwash deposits are nearly level, coarse textured, with low total nitrogen and low base saturation (Cole and Gessel 1965). Cation exchange capacity is low, ranging from 100 $\mu$equiv$\cdot$g$^{-1}$ in surface horizons to about 20 $\mu$equiv$\cdot$g$^{-1}$ at the 1 m depth. Coarse fragments (>2 mm) exceed 66% of soil volume in all horizons.

The Wilkeson silt loam is a colluvial soil mixed with lake sediments and at the study site sloped about 10° to the south. Base saturation averages 33% in surface horizons; cation exchange capacity of surface layers averaged 400 mequiv$\cdot$g$^{-1}$ (Bourgeois 1973). Coarse fragments occupy less than 10% of soil volume.

Dominant and codominant trees in the overstory on the poor site had a mean height of 23 m; average diameter at 1.4 m (dbh) above the soil surface was 27 cm. The 50-year site index for this stand was 80 (King 1966). The dense understory was dominated by *Gaultheria shallon* (Pursh) and *Mahonia nervosa* (Pursh), both woody shrubs.

Overstory trees on the good site averaged 33 m in height and averaged 31 cm dbh. The 50-year site index for this stand was 130. The relatively sparse understory consisted mostly of scattered *Polystichum munitum* (Kaulf) Presl. and occasional herbs.

## Methods

### *Belowground sampling: fine and small root biomass*

Root biomass (<5 mm) in both stands was detemined by sorting fine roots from soil cores taken during mid-June, mid-September, and mid-December 1977 and late March 1978. Soil cores were obtained by driving a sharp-edged steel tube, 10.2 cm inside diameter, into the soil to a depth of 45 cm. Twenty soil cores were taken from each stand at each sampling date. Sampling sites were located on 1 × 1 m grids surveyed in each stand using a table of random numbers to select grid intersections where sampling was done. Individual cores were placed in polyethylene bags and returned to the laboratory for sorting.

In the laboratory, roots were separated from other organic material and mineral soil by passing the soil cores through a sequence of five sieves with hole sizes ranging from 12.7 to 2.0 mm. Live and dead root material was hand sorted from the residue remaining on each sieve. Preliminary studies indicated virtually no roots passed through the 2-mm sieve. Live and dead roots were distinguished on the basis of color and texture. Dead roots were dark and spongy; living roots were pinkish and firm. In case of doubt, roots were broken and examined under magnification for color and cohesion between the cortex and pericycle. In dead roots, the stele could easily be pulled from the cortex; this was not possible with living roots. Few roots required close examination.

Live and dead roots were separated into two size categories. Roots less than 2 mm in diameter were termed *fine* roots. Roots between 2 and 5 mm in diameter were termed *small* roots. Sizing was done by visually comparing root diameters with sections of wire having diameters of 2 mm and 5 mm. Accuracy of visual estimates was periodically checked by measuring roots with vernier calipers. Once sized, all fine and small roots were dried at 75°C, weighed, then ashed at 450°C in a muffle furnace for 24 h and reweighed. Live root (biomass) and dead root (necromass) are reported as ash-free dry weight.

### *Stand measurements: aboveground and coarse root biomass*

A 20 × 20 m plot was established in each stand. Diameter at breast height (1.4 m) was measured on all stems within each plot. Sapwood thickness and radial stem increment for the past 5 years were determined from increment cores removed at breast height. One dominant and four codominant trees were selected in each plot for height measurements. Two branches were removed from each of four codominant trees to determine average needle retention time.

Biomass of aboveground tree components and coarse roots was estimated from logarithmic regressions of tree dry weight on stem diameter (Dice 1970; Riekerk 1967). Basic procedures are described by Grier and Logan (1977). Foliage biomass was determined for each stand using linear regressions of leaf biomass on sapwood basal area (Grier and Waring 1974).

### *Stand measurements: net primary production*

Net primary production (NPP) was estimated by measuring the major components of the equation: NPP = $\Delta B$ + M, where $\Delta B$ is annual biomass increment and $M$ (mortality) represents annual losses to plants by mortality or shedding. Other components of primary production such as branchfall and herbivory were not measured. In stands of this age these components of production should be relatively small and similar in both stands.

### *Biomass increment*

The 1977 stem diameters were obtained by subtracting 1977–1978 stem diameter increment from diameters measured in 1978. This was done for each tree on both plots. Stem radial wood increments measured from increment cores were adjusted to include radial bark increment using a procedure described by Grier and Logan (1977). Regression equations were then used to compute biomass for both 1977 and 1978 diameters. Stemwood, stembark, live branch, and coarse root biomass increment were calculated by subtracting 1977 biomass from 1978 biomass. Leaf biomass, computed using linear regressions on sapwood basal area, did not change appreciably in either stand between 1977 and 1978. This indicated the leaf biomass was at or near steady state in both stands.

### *Mortality*

Litter fall was estimated after determining the average needle retention time to be 5 years in each stand. Annual litter-fall production was estimated to be 20% of foliar biomass.

Annual fine root losses by death or shedding were estimated using two different methods. In the first procedure, turnover of roots (<5 mm) was calculated by simply subtracting the seasonal high biomass from the seasonal low. Differences in mean root biomass were evaluated for statistical significance using the standard $t$-test at $p < 0.05$.

### *Root growth observation and measurement*

Turnover of fine (<2 mm) roots were also estimated by combining data obtained by soil coring with that from observation of root growth. Four randomly located Plexiglas root observation windows were installed in the soil of each study plot; each window had an area of 0.76 $m^2$. All windows were set 10–20 mm from a clean soil pit face. The air space between the Plexiglas and the soil was filled in such a way as to reconstruct the original soil profile with sieved soil. To prevent unnatural soil temperature and humidity fluctuations, observation pits were covered with 15 cm thick, spun glass insulation stapled to plywood covers.

Root appearances, mortality, and elongation were determined every 2 weeks. A ratio of the number of new root appearances to the number of existing roots which ceased elongating, became discolored, and failed to regrow was calculated. This ratio was divided into the peak fine to obtain a second estimate of root turnover.

## Results

### *Fine and small root biomass*

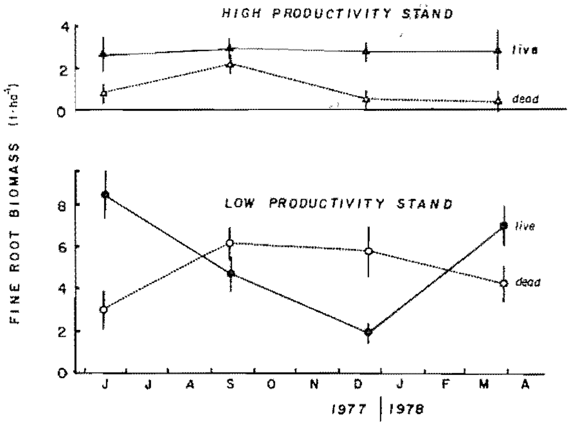

FIG. 1. Seasonal representation of live and dead fine root biomass (<2 mm in diameter) from soil coring in two 40-year-old Douglas-fir stands growing on soils of contrasting productivity. Estimates are given ± 1 SE ($n$ = 20).

Marked seasonal fluctuations in fine root biomass were observed in soil cores obtained from the stand occupying the low productivity site. Living fine root biomass reached a peak of 8.3 $t\cdot ha^{-1}$ in June, declined to a low of 2.1 $t\cdot ha^{-1}$ in December, and increased to 7.3 $t\cdot ha^{-1}$ by late March (Fig. 1) (at $p < 0.05$). Mean values on all sampling dates were significantly different from one another. Fine root necromass also changed seasonally on the low productivity site. This appeared to be related to the changes in fine root biomass. Thus as fine root biomass decreased in autumn, fine root necromass increased. When fine root biomass increased in the spring, fine root necromass decreased slightly, presumably owing to decomposition.

Fine root biomass in the stand occupying the high productivity site did not change appreciably from sampling to sampling. Fine root necromass in the stand on the high productivity site showed a significant increase in the fall sampling. Moreover, live fine root biomass of the stand occupying the high productivity site averaged less than half that noted for the stand occupying the low site except in the winter when their productivities were equal (Fig. 1).

No statistically significant differences were noted between the high and low productivity stands for living or dead small roots. Similarly, there were no significant differences between small root biomass estimates on different sampling dates for either site. Small root biomass in both stands was less than fine root biomass. The proportion of small root biomass to fine root biomass in the stand occupying the poor site was slightly greater than that of the good site.

### *Fine and small root turnover*

Fine root production and turnover on the low productivity site was approximately two and a half times

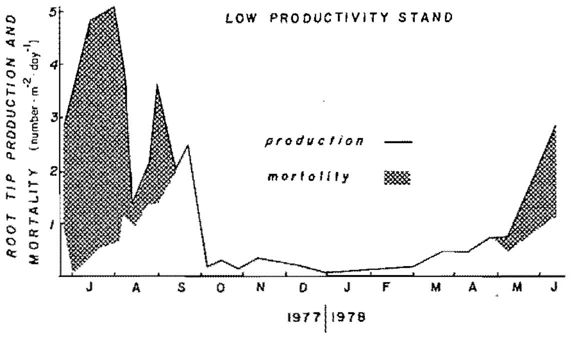

FIG. 2. Mean values for the seasonal production and mortality of fine and small roots which appeared on four root observation windows installed in the stand growing on the low productivity site.

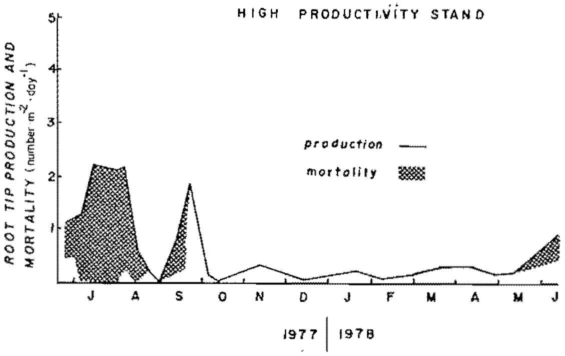

FIG. 3. Mean values for the seasonal production and mortality of fine and small roots which appeared on four root observation windows installed in the stand growing on the high productivity site.

that on the high productivity site. Estimates obtained using the two different methods were comparable for individual sites. It should be noted that both procedures used in this study for evaluating fine root turnover should yield conservative estimates as fine root production and turnover taking place between soil corings or observation dates could not be determined.

Fine root turnover was first estimated by taking the difference between significantly different mean fine root biomass. In the stand occupying the low productivity site this posed no problem because of large seasonal fluctuations in fine root biomass (cf. Fig. 1). In the low productivity site the peak fine root biomass of 8.3 t·ha$^{-1}$ in June was about four times the low value of 2.1 t·ha$^{-1}$ observed in December. Assuming the annual production and turnover from one year to the next do not change (i.e., annual production = annual turnover), fine root necromass production was estimated by the difference, to be 6.2 t·ha$^{-1}$.

As there were no significant differences in fine root biomass throughout the year on the good site, it was not possible to determine fine root production by difference. However, small but statistically significant seasonal fluctuations in fine root necromass indicated that fine root production by the stand on the high productivity site was at least 1.6 t·ha$^{-1}$. This is likely an underestimate since weight loss from dead roots by decomposition was not accounted for.

Root tip appearances and mortality, combined with peak fine root biomass data, were used to produce a second estimate of fine root turnover. Root observation window data (Figs. 2 and 3) showed bimodal seasonal patterns of root tip production in both stands. The rate of root tip production was 2.5-fold greater on the low productivity site. Root tip mortality was likewise less on the high productivity site. Averaged over the study period a similar percentage of root tip mortality was observed on the observation windows in both the low productivity (63%) and high productivity site (65%) stands. Figures 2 and 3 indicate that although root production and mortality patterns were similar in both sites, root tip and turnover in the low productivity site was about three times that on the high productivity site. Fine root turnover calculated from observation window data was 5.2 t·ha$^{-1}$ on the poor site and 1.6 t·ha$^{-1}$ on the good site.

Because of the much larger sampling variation in biomass estimates of small root turnover differences were not statistically significant. However, these values are included to indicate the possible range for each stand.

### *Total stand biomass*

Aboveground biomass of the low site was 239.6 t·ha$^{-1}$ (81.2% of total stand biomass); the aboveground biomass of the high site was 453.3 t·ha$^{-1}$ (84.2% of total). The major components contributing to this difference were stem wood and stem bark (Table 1).

Belowground biomass was not similarly proportioned. On the low site, 19% of the total biomass including roots was in belowground components. Total root biomass was 16% of stand biomass on the the high site. Although aboveground biomass was twice as large on the good site, the poor site had proportionately more biomass in its root structures, especially the fine roots in which the Douglas-fir on the low productivity site had invested three times the biomass compared with the high-productivity site Douglas-fir.

### *Total stand net primary production*

Aboveground and coarse root biomass increment on the poor site was approximately half (6.4 t·ha$^{-1}$) that of the good site (12.1 t·ha$^{-1}$) (Table 2). However, the stand on the low productivity site expanded a larger share of its dry matter production on fine root turnover than did the stand on the high productivity site.

In contrast, fine root turnover was a large component

TABLE 1. Above- and below-ground biomass in two 40-year-old Douglas-fir stands on low and high productivity sites at Charles Lathrop Pack Experimental Forest, Washington

| Component | Low site (t·ha$^{-1}$) | % of total | High site (t·ha$^{-1}$) | % of total |
|---|---|---|---|---|
| Stem wood[a] | 188.5 | 61.5 | 368.8 | 66.4 |
| Stem bark[a] | 33.0 | 10.8 | 55.2 | 9.9 |
| Living branch [a] | 17.1 | 5.6 | 27.7 | 5.0 |
| Foliage[b] | 10.0 | 3.3 | 16.0 | 2.9 |
| Coarse root[c](≥5 mm) | 47.1 | 15.4 | 83.6 | 15.0 |
| Small root[d] (2–5 mm) | 2.2 | 0.7 | 1.8 | 0.3 |
| Fine root[d] (≤2 mm) | 8.3 | 2.8 | 2.7 | 0.5 |
| Total | 306.2 | 100 | 555.8 | 100 |

[a] Dice (1970).
[b] Grier and Waring (1974).
[c] Rierkerk (1967).
[d] This study, maximum seasonal.

TABLE 2. Total net primary production in tons per hectare for two 40-year-old Douglas-fir stands

| Component | Low site | % of total | High site | % of total |
|---|---|---|---|---|
| Stem wood[a] | 4.2 | 27.3 | 8.2 | 46.0 |
| Stem bark[a] | 0.9 | 5.8 | 1.7 | 9.5 |
| Living branch[a] | 0.2 | 1.3 | 0.6 | 3.4 |
| Foliage[b] | 2.0 | 13.0 | 3.2 | 18.0 |
| Coarse root[c] (>5 mm) | 1.1 | 7.1 | 1.6 | 9.0 |
| Small root[d] (2–5 mm) | 1.4 | 9.1 | 1.1 | 6.2 |
| Fine root[e] (<2 mm) | >5.6 | 36.4 | >1.4 | 7.9 |
| Total | 15.4 | 100 | 17.8 | 100 |

[a] Dice (1970).
[b] This study assuming litter fall equals 20% of standing crop.
[c] Rierkerk (1967).
[d] This study, maximum root biomass – minimum root biomass (not statistically significant).
[e] This study, average of two methods.

of NPP on the low productivity site. A conservative estimate of 5.6 t·ha$^{-1}$, or over 36% of NPP, went into the production and turnover of fine root structures in this stand. Total root production including biomass increment by coarse roots and small root production is 8.1 t·ha$^{-1}$ for about 53% of the stand's total net production on the low site.

## Discussion

In this study, fine root biomass for the low productivity site as determined in this study fluctuated within the range of values reported for North American conifers. The seasonal high fine root biomass (<2 mm) on the low productivity site (8.3 t·ha$^{-1}$) is less than the 11.3 t·ha$^{-1}$ (<5 mm) found by Santantonio (1977) working with the same species but in older stands. However, his reported value is very similar to that of the low site (10.5 t·ha$^{-1}$) in the present study if the small roots (2–5 mm) are included. In contrast, Safford and Bell (1972) found white spruce fine root biomass (<3 mm) was 6.96 t·ha$^{-1}$, while ponderosa pine was found to have a fine root biomass (<5 mm) of 4.5 t·ha$^{-1}$ (Moir 1965). Fine root biomass on the good site is below values reported for other stands in North America, except for Kimmins and Hawkes (1978).

Differences between fine root biomass and net production values reported in this study and those of other studies result from a variety of procedural methods in addition to site-specific considerations. As can be observed above there is no strict convention in size classification of fine root biomass. Most researchers have considered fine roots to be no more than 5 mm in diameter. Small roots (2–5 mm) are included in this study for comparison with work in Oregon by

Santantonio et al. (1977) on the same species. Without any detailed knowledge of seasonal production and turnover patterns the reliability of a single (static) determination of fine root biomass depends heavily on the date and intensity of sampling. Comparisons with other ecosystems should be undertaken with due caution as in many studies there have been little or no attempts to distinguish live from dead roots the inevitable inclusion of fine root necromass into reports of fine root standing crop.

Distinctly different patterns in the annual partitioning of dry matter production were observed in stands of the same age but growing on soils with apparently large differences in productivity potential. On the higher productivity site the stand channeled most of its net production into biomass increment. For Douglas-fir growing on this site, production of new roots and foliage to secure adequate water, nutrients and sunlight needed in growth was a small but significant fraction (26%) of the total dry matter produced during the year. Higher productivity on this site means primarily more aboveground biomass increment.

In contrast, on the low productivity site approximately 60% of annual net production did not accumulate as biomass, but instead was used to develop short-lived roots. On an annual basis, a large portion of these roots died and became an energy source for decomposers. "Low productivity" in this sense can be construed to mean poor aboveground growth.

Total net primary production differed by only 13% in these stands when both above- and below-ground compartments of these stands were examined. Although this phenomenon as yet has not been substantiated by other comparative investigations the implications are that terrestrial productive potential from site to site may be smaller than previously suspected. Without periodic examination of fine root dynamics the belowground contribution to total net primary production may be drastically underestimated in many world ecosystems. On what was thought to be low productivity sites, aboveground growth was reduced in favor of expending more energy belowground to develop and maintain uptake structures. On harsh sites which may impose water or nutrient deficiencies this shift in production allocation from above to belowground may be an essential mechansim to avoid or alleviate stress.

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